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Diet segregation in Adélie penguins: some individuals attempt to overcome colony-induced and annual foraging challenges

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ABSTRACT: Intraspecific competition for food can be especially high in colonial breeding seabirds. To minimize colony-induced or annual foraging challenges, diet may vary among individuals, but few studies have simultaneously investigated the effects of both extrinsic conditions (e.g. colony or year effects) and parameters of an individual (e.g. sex, age or individual quality) on diet in seabirds. Using stable isotope analyses, we studied the diet of 214 Adélie penguins *Pygoscelis adeliae* of known sex, age and breeding quality, nesting in 2 colonies on Ross Island, Antarctica, over 3 breeding seasons. During the study, $\delta^{15}N$ and $\delta^{13}C$ isotope values were lower in penguins breeding at Cape Crozier compared to those at Cape Bird, revealing a difference in prey proportions. Cape Bird penguins were estimated to consistently consume more energy-rich silverfish *Pleuragramma antarctica*, while birds at Cape Crozier ate more crystal krill *Euphausia crystallorophias*. We also found inter-annual differences in diet, with a higher dietary fish proportion in both colonies during 2011. Males had significantly higher $\delta^{15}N$ values, indicating a higher fish consumption than females. This sexual segregation in diet was particularly pronounced at Cape Bird, where the overall isotopic niche was wider than at Cape Crozier. Differences in diet among adults of varying ages only existed at Cape Bird, where middle-aged penguins consumed more fish than old and young penguins. This study provides evidence that Adélie penguin diet is largely driven by annual, seasonal and local abundances of prey, with only some individuals selectively foraging for more nutritional prey if prey choices are present.

KEY WORDS: Adélie penguin · Crystal krill · Diet segregation · Intraspecific competition · Ross Sea · Silverfish

1. INTRODUCTION

The principle of competitive exclusion states that species competing for the same resources cannot stably co-exist in the long-term (Gause 1934). Hence, in communities where several different species compete for limited food resources, foraging is usually spatially (e.g. Arlettaz 1999, Masello et al. 2010)

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and/or temporally (e.g. Cotton 1998, Blázquez et al. 2009) segregated in order to avoid intense interspecific competition. Sympatric species foraging at the same time can also partition their food resources by having different diets (Luiselli & Rugiero 1991, Estes et al. 2003). The same mechanisms that minimise interspecific competition for food (i.e. partitioning of resources in space, time or through diet) also mitigate resource competition within species, with the combination of both interspecific and intraspecific competition strongly affecting population demographics and community structure (Creese & Underwood 1982, Estes et al. 2003). As individuals within one species usually have a similar spatial and temporal preyscape (i.e. composition and distribution of prey within their habitat), it has been suggested that intraspecific competition can be more intense than interspecific competition (Begon et al. 2006). Therefore, in most animals, foraging space is partitioned into home ranges or territories between individuals, pairs or families, at least during the reproductive season, when reliable food resources are needed to raise offspring (Brown & Orians 1970).

Contrasting with this, many species of seabirds are central-place foragers that share a feeding area during the breeding season (Orians & Pearson 1979, Schoener 1979). They usually nest in large colonies (Rolland et al. 1998) on cliffs or islands, and they exploit marine food resources in the adjacent sea (e.g. Shealer et al. 2002). Individuals within a colony generally use the same foraging space — a colony-specific foraging area (i.e. Ashmole's halo; Ainley et al. 2004, Gaston et al. 2007) — and depending on colony size, intraspecific competition for food can be especially high (Ainley et al. 2004, Grémillet et al. 2004). Such intra-population competition can lead to the evolution of sexual segregation (i) of the foraging space, both horizontally (foraging area) and vertically (water column depth) (Cook et al. 2007, Weimerskirch et al. 2009); (ii) of the time of foraging (Cook et al. 2007, Weimerskirch et al. 2009); and (iii) in diet (Kato et al. 1996, Bearhop et al. 2006). It has been suggested that these sex-related differences in foraging behaviour and diet are often related to size dimorphism (Phillips et al. 2011), whereby morphological characteristics (e.g. larger size) allow one sex to exploit resources that are unobtainable by the other (Forero et al. 2005, Bearhop et al. 2006). Among diving species, some evidence indicates that larger birds can dive deeper and forage on larger prey (Gorman et al. 2014, Paredes et al. 2015). However, body size may not necessarily explain all differences in foraging behaviour or diet between males and females (Lewis et al. 2002, Quillfeldt et al. 2011), and thus there is a need to investigate alternative mechanisms that may underlie any observed sexual variation in foraging behaviours and diet.

In comparison to sexual segregation in foraging behaviour and diet, partitioning of food resources between different aged individuals or age classes is less documented in seabirds. Evidence exists from several studies that diet varies to some degree among age classes (i.e. chicks, juveniles and adults; e.g. Schmutz & Hobson 1998, Hodum & Hobson 2000, Forero et al. 2002). For instance, in some seabird species, provisioned chicks were found to have a higher trophic level diet than their parents (Hodum & Hobson 2000, Forero et al. 2002, Cherel 2008), suggesting that parents may adjust their foraging strategies to meet the nutritional demands of their growing offspring (Pierotti & Annett 1991). In contrast, foraging for themselves, 1-yr-old Magellanic penguins *Sphensicus magellanicus* had a considerably lower trophic level diet than adults (Forero et al. 2002). Differences in diet among adult seabirds with respect to age and/or breeding experience have rarely been investigated (but see Forero et al. 2005, Pelletier et al. 2014), although reproductive success often increases with age and/or experience, at least during the early years of breeding (e.g. Weimerskirch 1992, Mauck et al. 2004). As birds age, they acquire experience in locating and/or catching prey and, thus, their improvements in foraging proficiency affect their own diet and allow them to deliver more and better-quality food to their offspring (Forslund & Pärt 1995, Daunt et al. 2007). If this is the case, then diet is expected to vary with age/experience. However, breeding performance does not necessarily increase with age: in several seabirds, some individuals (referred to as 'higher-quality' individuals) are consistently better at rearing offspring than others, regardless of their age or experience (Annett & Pierotti 1999, Lescroël et al. 2009). The consistently higher reproductive performance of some individuals can be linked, at least in part, to proficient foraging (Lescroël et al. 2010) and a higher-quality diet (Pierotti & Annett 1991, Annett & Pierotti 1999). Variation in reproductive performance and foraging success among individuals has been shown to be particularly pronounced during resource-poor seasons, whereby older, more experienced or higher-quality individuals are capable of adjusting their behaviour to compensate to some degree for poorer foraging conditions, while younger or lower-quality individuals are less able to do so (Daunt et al. 2007, Lescroël et al. 2010).

As the degree of difficulty to locate and capture prey is partly dependent on how many individuals compete for a limited, local food resource, breeding in a large colony may add to challenging foraging conditions for individuals. Marine food resources surrounding large colonies are depleted much earlier in the season (Ainley et al. 2004, 2015) and individuals breeding in those colonies must travel farther and/or dive deeper than those of smaller-sized colonies (Ford et al. 2015). Hence, partitioning of food resources between individuals of different sex, age or quality may be more likely to occur among individuals of large colonies. In addition, partitioning of food resources is expected to occur only in areas where there are a variety of prey species of a limited abundance (i.e. no single prey species is abundant enough to feed all predatory individuals). In Antarctica, the distribution and abundance of prey, such as crystal krill *Euphausia crystallorophias* and Antarctic silverfish *Pleuragramma antarctica*, is highly patchy, because sea ice cover in an area varies in extent and is known to affect the availability of these pagophilic prey species (Sala et al. 2002, La Mesa et al. 2010, 2015, La Mesa & Eastman 2012). Depending on local and seasonal abundances of prey species, the occurrence of intraspecific diet segregation in predators may be more plastic than has been previously acknowledged. The question is whether some individuals can overcome colony-induced or seasonal foraging challenges by selecting different prey, and if so, which individuals are able to do so (i.e. older, higher-quality individuals or members of a particular sex). However, to date, few studies have simultaneously investigated the effects of both extrinsic conditions (e.g. colony, year effects) and parameters of an individual (e.g. sex, age and individual quality) on diet choice in seabirds (but see Bearhop et al. 2006, Michalik et al. 2013).

In order to disentangle these effects, we studied the diet of adult Adélie penguins *Pygoscelis adeliae* over 3 consecutive austral summers (2010–2011, 2011–2012 and 2012–2013) at Cape Bird and Cape Crozier on Ross Island, Antarctica (Fig. 1). The 2 colonies are 75 km apart, and the colony at Cape Crozier (with 260 000–280 000 breeding pairs during the present study) is almost 4 times the size of the Cape Bird colony (60 000–75 000 pairs; Lynch & LaRue 2014, Lyver et al. 2014). Both colonies have steadily increased in size from 2000 onwards (Lyver et al. 2014). Stable carbon and nitrogen isotope ratios obtained from penguin red blood cells were used as a proxy of diet. Nitrogen isotope ratios ($\delta^{15}N$) largely reflect the trophic level of assimilated prey (e.g. Minagawa & Wada 1984, Olive et al. 2003), while carbon isotope ratios ($\delta^{13}C$) can be used to assess foraging location as they vary relative to ocean productivity, and thus differ between inshore and offshore and pelagic versus benthic food webs (reviewed in Rubenstein & Hobson 2004). The $\delta^{13}C$ of particulate organic matter in Antarctic waters also differs with latitude and the occurrence of sea ice (Rau et al. 1991). Adélie penguins in the southern Ross Sea mainly forage on 2 prey species that differ markedly in energy density and isotopic values (Ainley et al. 2003, 2018): the energetically more rewarding Antarctic silverfish ($\delta^{15}N = 10.2 \pm 0.5$‰, 5.0 kJ g^{-1}; Lenky et al. 2012, Pinkerton et al. 2013) and the less energy-rich crystal krill ($\delta^{15}N = 6.5 \pm 0.6$‰, 4.6 kJ g^{-1}; Ainley et al. 2003, Pinkerton et al. 2013). We analysed sea ice conditions at both colonies, because sea ice cover in the area is likely to influence crystal krill and silverfish availability (Sala et al. 2002, La Mesa et al. 2010, 2015, La Mesa & Eastman 2012). As previous studies found seasonal, inter-annual and colony effects on diet (Ainley et al. 2003, 2018, Tierney et al. 2008), we expected that diet would vary by year and

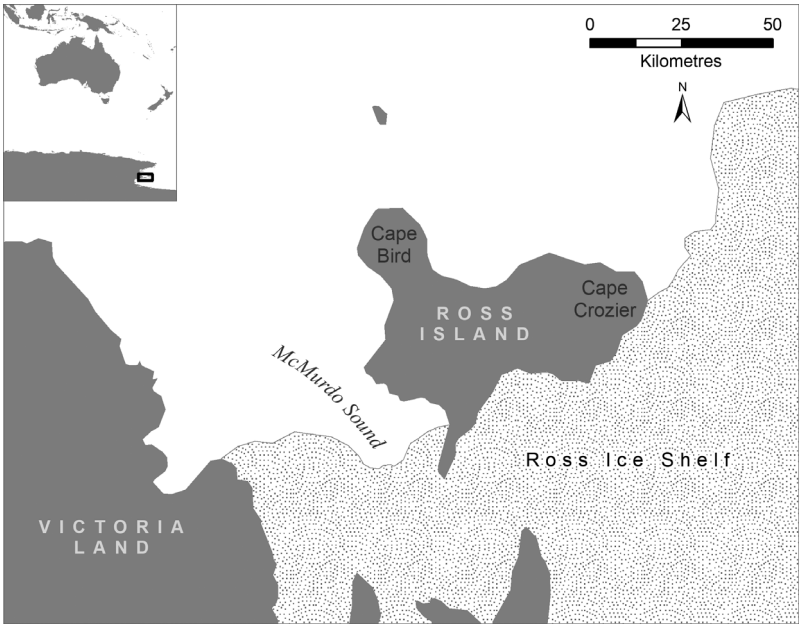

Fig. 1. The diet of adult Adélie penguins was studied over 3 consecutive austral summers (2010–2011, 2011–2012 and 2012–2013) at Cape Bird and Cape Crozier on Ross Island, Antarctica. The colony at Cape Crozier is almost 4 times the size of the Cape Bird colony

colony. However, in the present study we also tested whether some individuals of a particular sex, age or breeding quality can overcome these broader year or colony effects. We first investigated whether there are differences in diet between the sexes. As silverfish occur deeper than crystal krill in our study area (Ainley et al. 2015), we hypothesised that females would prey more on krill than males as their smaller body size may not allow them to dive as deep as males (e.g. Schreer et al. 2001). We also tested for interaction effects between sex, colony and year, because it is possible that the diet of males and females only differs in particular locations or years relative to environmental conditions. We then tested whether age or quality of individuals influences diet. We hypothesised that older or better-quality individuals, which forage more proficiently (Lescroël et al. 2010), would feed preferentially on larger, more energy-dense prey (e.g. silverfish), given that a greater proportion of fish in the diet leads to more robust chicks, enhancing their subsequent survival (Chapman et al. 2011, Whitehead et al. 2015, Jennings et al. 2016, Ainley et al. 2018).

2. MATERIALS AND METHODS

2.1. Study site and sample collection

Adélie penguin *Pygoscelis adeliae* diet, as proxied by stable carbon and nitrogen ratios, was studied during the early chick-rearing stage over 3 consecutive austral summers (2010–2011, 2011–2012 and 2012–2013) at Cape Bird and Cape Crozier in Antarctica (Fig. 1). Hereafter, field seasons are indicated by the first year of the austral summers. Fledglings from these populations have been marked using stainless-steel flipper bands embedded with a unique 5-digit number as part of a long-term demographic study (Dugger et al. 2006); thus, the ages of all adult penguins included in this study were known. In addition, individual breeding histories of banded penguins were known from previous research, because both colonies are extensively searched and monitored annually to find and record nesting success of banded penguins. Hence, we had data on the number of seasons each banded penguin was present in the colony and attempted to breed (e.g. eggs were laid), how many eggs were laid in each individual's nest, and whether at least one chick was raised to the 'crèche' stage (when chicks are thermally independent and can be left alone while both parents forage simultaneously). The breeding quality index (BQI) for each banded individual was calculated as described by Grémillet et al. (2018). We first determined the probability of breeding success using 4 independent variables: age, previous breeding experience, colony of origin and breeding year. We verified that the independent variables were not highly correlated (e.g. $r > 0.7$) and that the most general model fit the data. The BQI of each individual was then calculated by determining the difference between the actual mean breeding success per individual and the predicted breeding success for every year during which a given individual had been resighted when at least 3 yr of age, up to the year in this study. Negative BQI values indicate lower than average long-term breeding performance, while positive values indicate above average long-term breeding performance.

Each penguin included in this study was blood sampled once during 1 of 3 study seasons to determine stable isotope ratios as a measure of their diet over the previous 3–4 wk (see below) and to molecularly sex each individual. Each sampled bird had just returned from sea to feed their offspring. In 2010, 55 penguins were sampled in the period from 19 Dec 2010 to 10 Jan 2011 (21 sampling days); in 2011, 82 penguins were sampled in the period from 23 Dec 2011 to 8 Jan 2012 (17 sampling days); and in 2012, 77 penguins were sampled in the period from 20 Dec 2012 to 13 Jan 2013 (24 sampling days). Therefore, timing of blood sampling was consistent among years. All samples were taken when penguins were brooding or guarding their chicks and before the crèche stage. Adult penguins were captured by hand on their nest sites, and 2–5 ml of blood was collected from their right jugular vein with a sterile 21 gauge needle and 5 ml syringe within 1–3 min after capture. After blood sampling, pressure was applied using sterile gauze to stop any bleeding. We then measured their flipper length to the nearest 1.0 mm, torso circumference to the nearest 0.5 cm and mass to the nearest 25 g. Chicks were kept warm and safe during blood sampling of adults, and were placed back in nests, shortly before their parent was released. Each parent returned immediately to the nest. Handling times for penguins ranged between 5 and 10 min from capture until release. One drop of fresh blood was placed on a filter paper that was later used to determine the sex of penguins using molecular techniques (Fridolfsson & Ellegren 1999). The remaining blood was centrifuged for 10–15 min to separate the serum from the packed blood cells. A micropipette was used to transfer the serum into a new micro tube. Serum and packed blood cells were then frozen at –20°C until all packed

blood cell samples were freeze-dried for subsequent lab work (sample sizes in Table 1).

2.2. Stable isotope analyses

We used previously published stable isotope values for the 2 main prey species in our study area. Pinkerton et al. (2013) collected 48 juvenile (90–151 mm) *Pleuragramma antarctica* within our study area and determined $\delta^{13}C$ as −25.1 ± 0.8‰ and $\delta^{15}N$ as 10.2 ± 0.5‰. We used stable isotope values of juvenile *P. antarctica*, because this is the size class most consumed by Adélie penguins (Ainley et al. 2003). Stable isotope values of 244 crystal krill *Euphausia crystallorophias* collected in our study area were $\delta^{13}C$ = −25.0 ± 1.2‰ and $\delta^{15}N$ = 6.5 ± 0.6‰ (Pinkerton et al. 2013). We analysed nitrogen and carbon stable isotopes of penguin red blood cells (erythrocytes). In captive penguins, stable isotope ratios of red blood cells provided dietary information integrated over a period of a month (Barquete et al. 2013), although we suspect that metabolic rates and turnover times in active wild penguins are higher than in captive penguins. Carbon and nitrogen isotope analyses were carried out on samples of 0.65–0.7 mg aliquots (weighed into tin cups) of freeze-dried red blood cells. Carbon and nitrogen isotope ratios were measured simultaneously by continuous-flow isotope ratio mass spectrometry (CF-IRMS) at the University of California, Davis, Stable Isotope Facility, using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd). Laboratory standard measurements were previously calibrated against NIST. Standard Reference Materials indicated that the standard deviation is 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from the international standards V-PeeDee Belemnite for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$.

2.3. Data analyses

2.3.1. Sea ice conditions

Using microwave satellite images of the first cloud-free day of each week, an index of sea ice cover (average ice cover estimate for all pixels) per week was established for each colony's respective foraging area for the duration of the sampling period each year. Image analyses were performed in ArcGIS (ESRI 2006) using AVHRR (advanced very-high-resolution radiometer) and DMSP (Defense Meteorological Satellite Program) satellite images archived by the Arctic and Antarctic Research Center at the University of California San Diego. Data for end of December and January in 2011 were unavailable because of the cessation of a satellite sensor. The resolution of images varied between 0.5 and 1.5 km per pixel.

2.3.2. Diet composition

A Bayesian model in SIAR 4.0 (Stable Isotope Analysis in R; Parnell & Jackson 2013), conducted in R version 3.3.1 (R Development Core Team 2016), was applied to obtain diet composition estimates (for more details on this technique, see Masello et al. 2010 and Quillfeldt et al. 2015). The SIAR model incorporated sources of uncertainty, in particular the variability in isotope values of prey species (Inger & Bearhop 2008, Moore & Semmens 2008). SIAR applies Markov chain Monte Carlo methods within a Bayesian framework to assign consumers based on their isotope values to their dietary endpoints based upon a Gaussian likelihood with a Dirichlet prior mixture on the mean. The model assumes that each target value (i.e. the stable isotope values of each individual) comes from a Gaussian distribution with an unknown mean and standard deviation. The structure of the mean is a weighted combination of the food sources' isotopic values. The standard devi-

Table 1. Sample sizes of Adélie penguins, by sex and age class, from which blood was obtained to measure isotope values at Cape Crozier and Cape Bird in 2010–2012

Year	Cape Crozier						Cape Bird						Total
	Female			Male			Female			Male			
	Young	Middle	Old	Young	Middle	Old	Young	Middle	Old	Young	Middle	Old	
2010	5	5	2	5	4	11	3	2	3	5	4	6	55
2011	8	7	8	4	9	9	6	5	3	5	8	10	82
2012	9	9	3	4	7	7	8	4	3	14	6	3	77
Total	22	21	13	13	20	27	17	11	9	24	18	19	214

ation depends on the uncertainty around the fractionation corrections and the natural variability between target individuals within a defined group (e.g. a colony in a given year). We used the standard setting (20 000 iterations) and the isotopic discrimination rates for diet determined from blood in birds (reviewed in Caut et al. 2009). We used $\Delta^{15}N$ values of 2‰, and $\Delta^{13}C$ values of 0.2‰. Standard deviation was set to 0.5 for $\delta^{15}N$ and $\delta^{13}C$, a figure that is at the upper end of the range of values suggested by Caut et al. (2009).

The isotopic values of the 2 major prey sources, Antarctic silverfish and crystal krill, as described above and determined previously (Pinkerton et al. 2013), were included. In order to compare individual differences in prey selection, we ran SIAR models on individual penguin samples (using the siarsolomcmcv4 command), and obtained prey proportions for individuals.

The objective was to test our hypotheses regarding differences in penguin diet as a function of sex, age and breeding quality (using BQI as defined above). Due to limited sample sizes and use of categorical independent variables (e.g. year, colony, sex and age class; Table 1) by study design, we used generalized linear models (GLMs) to evaluate differences in penguin diet. Model selection procedures were also not performed due to low sample sizes, and it was not possible to apply a GLM to assess all the factors in a single model (e.g. age and sex with respect to year and colony). Separate models were run for $\delta^{15}N$, $\delta^{13}C$ and the proportion of crystal krill (as determined by SIAR), as each of these dependent variables provides different information about the diet. We included year and colony as independent variables to examine whether penguin diet differed between years and colonies as has been shown previously (Ainley et al. 1998, 2003). Each GLM included all 2- and 3-way interaction effects between year/colony and categorical independent variables (e.g. sex or age), as we hypothesised that diet segregation between sexes or different age classes may be more likely to occur in years or within colonies experiencing low food availability. Penguin age was categorised into 3 classes: young (3–6 yr of age), middle-aged (7–10 yr) and old (11–16 yr) birds (see Table 1). Our first GLM tested whether males and females have a different diet, and the second tested whether penguins of varying age or quality have a different diet. BQI was included as a continuous covariate in the GLM that examined diet differences with respect to penguin age class.

We compared the isotopic niches of penguins from the 2 colonies using SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). The location of the centroid indicates where the niche is centered in isotope space. A Bayesian approach based on multivariate ellipse metrics was used to calculate the Bayesian standard ellipse area (SEAb), which represents the core isotope niche width as described by Jackson et al. (2011). In addition, we calculated standard ellipse areas based on maximum likelihood (SEA), and corrected for sample size (SEAc). Ellipses were depicted using the draw.ellipse command of the R package plotrix, with the lengths of the 2 semi-major axes and the angle of the semi-major axis of the ellipse with the *x*-axis as parameters. To describe the spread of the data points, parameters proposed by Layman et al. (2007) were calculated. As proxies of intra-population trophic diversity, the mean distance to centroid and the mean nearest-neighbour distance were also calculated. Information on the trophic length of the community is given as the $\delta^{15}N$ range, and an estimate of the diversity of basal resources is provided by the $\delta^{13}C$ range. Means are reported ±SD, unless indicated otherwise.

3. RESULTS

3.1. Sea ice conditions

The percent sea ice cover of Cape Bird's foraging area from mid-December until mid-January (when blood isotope values were established) was consistently higher than the ice cover of Cape Crozier's for-

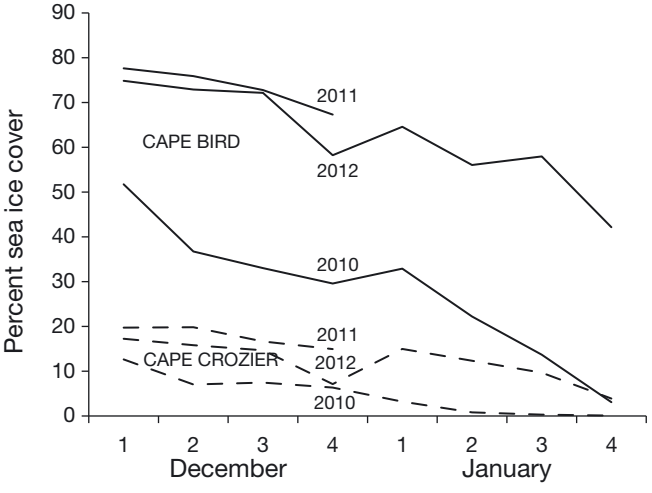

Fig. 2. Percent sea ice cover in the Adélie penguin foraging areas of the Cape Crozier (dashed lines) and Cape Bird (solid lines) colonies during December and of January in all 3 study seasons. Data for January 2012 were not available (see 'Materials and methods')

aging area during all 3 summer seasons (Fig. 2). Percent sea ice cover of Cape Crozier's foraging area during this period in all 3 years did not exceed 20%, while it ranged between 35% and 75% in the foraging area of Cape Bird (Fig. 2). Foraging areas of both colonies had the lowest sea ice cover in 2010 and the highest in 2011 (Fig. 2). For both foraging areas, sea ice cover exhibited the expected seasonal decrease over time.

3.2. Spatial and temporal variation in penguin diet

In total, we obtained isotopic values of 214 Adélie penguins *Pygoscelis adeliae* sampled at 2 colonies across 3 yr (Table 1). The diet of penguins differed significantly between the 2 colonies (all statistical results are available in Table 2, Figs. 3 & 4). Both the nitrogen and carbon stable isotope values were lower in penguins breeding at Cape Crozier compared to those at Cape Bird (Figs. 3 & 4A,B). Carbon stable isotope values in red blood cells were −26.20 ± 0.29‰ (min. −27.05‰, max. −25.42‰) for Adélie penguins at Cape Crozier and −25.25 ± 0.48‰ (min. −26.62‰, max. −24.22‰) for penguins at Cape Bird. Nitrogen stable isotope values were 9.31 ± 0.45‰ (min. 8.20‰, max. 10.30‰) for Adélie penguins at Cape Crozier and 9.60 ± 0.48‰ (min. 8.01‰, max. 10.76‰) for penguins at Cape Bird. This resulted in a difference in estimated prey proportions in SIAR mixing models that were consistent and statistically significant in all 3 seasons: Cape Bird penguins consumed more silverfish *Pleuragramma antarctica*, while Cape Crozier birds ate more krill *Euphausia crystallorophias* (Table 2, Figs. 4C, 5C). We also found inter-annual differences in diet, with a lower crystal krill proportion in both colonies during 2011 compared to the other 2 summers (Table 2, Fig. 4C). Notably, the nitrogen stable isotope values were significantly higher at both colonies in 2011 than in 2010 and 2012, indicating a higher consumption of fish in that year (Table 2, Fig. 4A). While there were also significant inter-annual differences in the carbon

Table 2. General linear models testing whether the diet, measured through $\delta^{15}N$, $\delta^{13}C$ and the proportion of crystal krill, differs between adult Adélie penguins of different sexes (male, female), from different colonies (Bird and Crozier), sampled in different years (2010, 2011, 2012); **bold values:** significance. SS: sum of squares; DF: degrees of freedom; MS: mean square

	SS	DF	MS	*F*	p (>*F*)
$\delta^{15}N$ (R^2 = 0.53)					
Intercept	17 275.1	1	17 275.1	160 546.8	<0.0001
Colony	4.7	1	4.7	44.1	**<0.0001**
Year	18.3	2	9.2	85.3	**<0.0001**
Sex	0.7	1	0.7	6.9	**<0.01**
Colony × Year	0.5	2	0.2	2.5	0.08
Colony × Sex	0.6	1	0.6	5.7	**0.01**
Year × Sex	0.2	2	0.1	1.2	0.29
Colony × Year × Sex	0.1	2	0.06	0.6	0.57
Error	21.7	202	0.1		
$\delta^{13}C$ (R^2 = 0.65)					
Intercept	128 486.4	1	128 486.4	954 474.7	<0.0001
Colony	48.6	1	48.6	360.7	**<0.0001**
Year	1.7	2	0.8	6.2	**<0.01**
Sex	0.2	1	0.2	1.2	0.28
Colony × Year	2.0	2	1.0	7.3	**<0.0001**
Colony × Sex	0.1	1	0.1	0.4	0.51
Year × Sex	0.1	2	0.1	0.5	0.63
Colony × Year × Sex	0.3	2	0.2	1.2	0.29
Error	27.2	202	0.1		
Crystal krill (R^2 = 0.59)					
Intercept	91.9	1	91.9	23078.9	<0.0001
Colony	0.34	1	0.34	86.76	**<0.0001**
Year	0.75	2	0.37	94.56	**<0.0001**
Sex	0.03	1	0.03	7.08	**0.008**
Colony × Year	0.04	2	0.02	4.69	**0.01**
Colony × Sex	0.02	1	0.02	5.86	**0.01**
Year × Sex	0.007	2	0.003	0.90	0.41
Colony × Year × Sex	0.003	2	0.0001	0.41	0.66
Error	0.80	202	0.003		

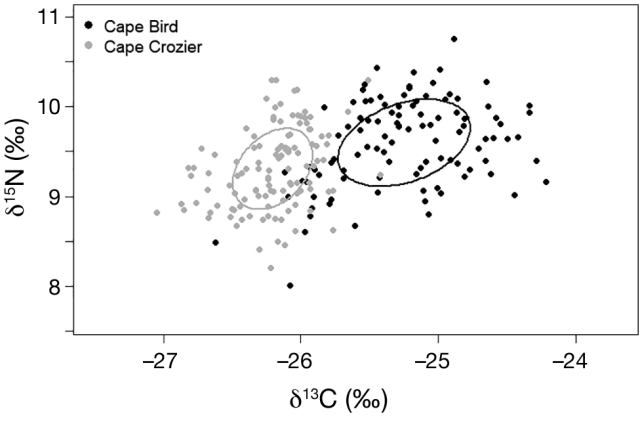

Fig. 3. Isotopic values (nitrogen [$\delta^{15}N$]; carbon [$\delta^{13}C$]) and standard ellipses marking isotopic niches of Adélie penguins breeding at Cape Bird (black symbols) and Cape Crozier (grey symbols)

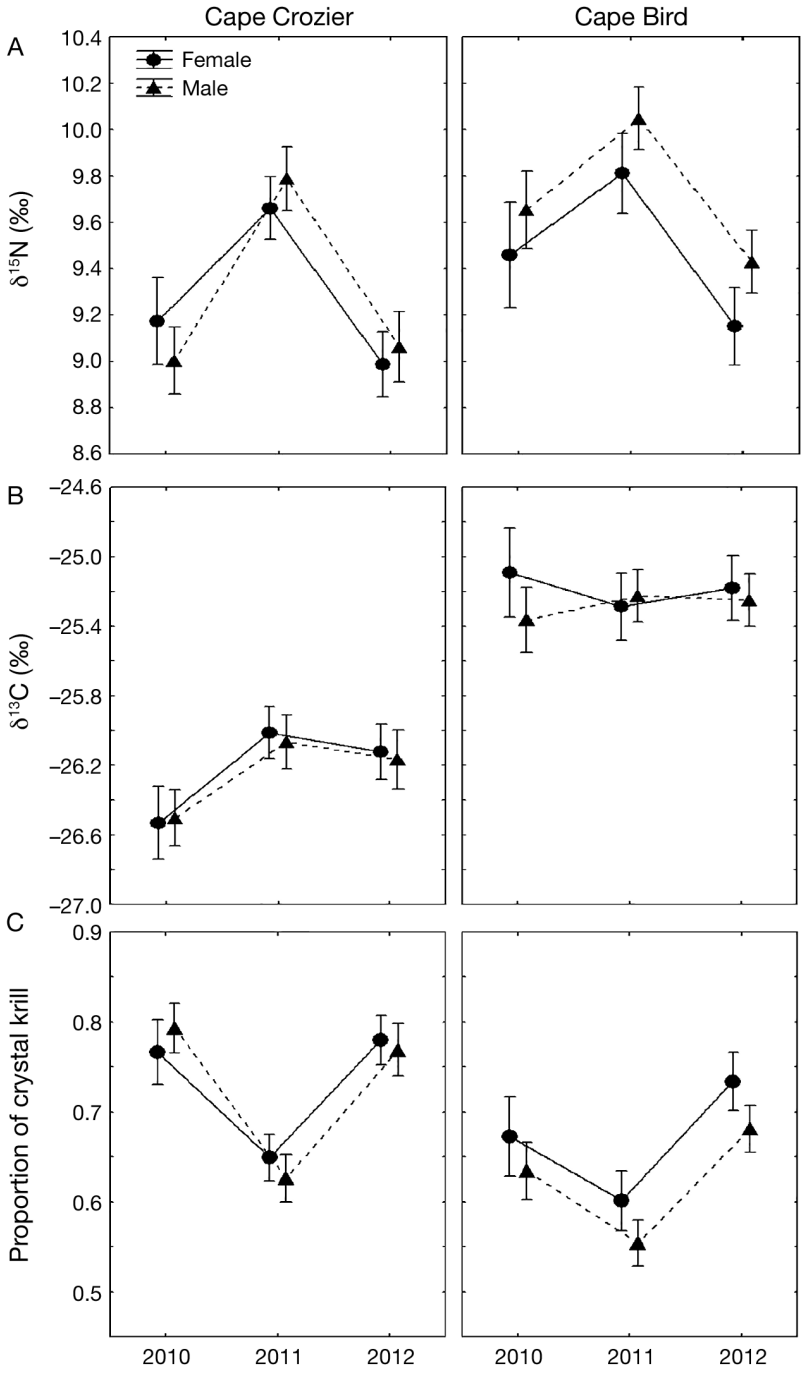

Fig. 4. Differences in (A) nitrogen isotope values ($\delta^{15}N$), (B) carbon isotope values ($\delta^{13}C$) and (C) proportions of crystal krill in the diet between female and male Adélie penguins. Means ± SD are shown

stable isotope values, this was mostly driven by yearly differences at Cape Crozier, where $\delta^{13}C$ values were lower in 2010 than in 2011 and 2012 (Table 2, Fig. 4B). In contrast, there was little interannual variation in $\delta^{13}C$ values at Cape Bird (Fig. 4B). Hence, the interaction between colony and year was highly significant for $\delta^{13}C$ values and the crystal krill proportion (Table 3). All isotopic niche parameters consistently indicated that Adélie penguins at Cape Bird had a wider niche than those breeding at Cape Crozier (Table 3, Fig. 3).

3.3. Sex-based differences in diet

Male penguins were significantly larger than females, both in respect to flipper length (males: 191.01 ± 6.20 mm; females: 186.15 ± 6.34 mm; $t = 5.67$, $p < 0.0001$) and torso circumference (males: 50.53 ± 2.32 cm; females: 48.41 ± 2.44 cm; $t = 6.49$, $p < 0.0001$). When we tested whether females and males differed in their diet (for statistical results, see Table 4), we found a sex difference in $\delta^{15}N$. While females and males had similar $\delta^{15}N$ values at Cape Crozier, at Cape Bird, males had higher $\delta^{15}N$ values than females (males: 9.51 ± 0.49‰ versus females: 9.37 ± 0.45‰; Fig. 4A), suggesting higher fish consumption in males. We found no sex-related differences in either $\delta^{13}C$ (males: −25.78 ± 0.63‰ versus females: −25.78 ± 0.61‰; Fig. 4B) or the calculated proportion of crystal krill (males: 67.28 ± 10.33% versus females: 70.22 ± 9.22%; Fig. 4C).

3.4. Diet differences in relation to age and breeding quality

Diet varied among young, middle-aged and old birds at Cape Bird, but not at Cape Crozier (for statistical results, see Table 4, Fig. 5). At Cape Bird, young birds consumed less fish (had lower $\delta^{15}N$ values, and a higher proportion of crystal krill in their diet) during all 3 summers in comparison to old and middle-aged birds (Table 4, Fig. 5A,C). Middle-aged birds consumed the most fish among those age classes. Carbon stable isotope values did not differ among the age groups (Fig. 5B). We also found no differences in diet among individuals with varying BQI (Table 4).

4. DISCUSSION

4.1. Diet differences in relation to sex, age and breeding quality

This study was conducted during the chick guard stage, when most Adélie penguins *Pygoscelis adeliae* within the colony have small to medium-sized chicks to feed, though the diet information reflected in the isotope analysis could represent prey that was acquired up to 4 wk earlier, potentially overlapping with the end of the incubation phase. During incubation and the guard stage, one parent stays at the nest, while the other forages at sea. During this period, the competition for food by this central-place forager begins to intensify. Moreover, as chicks age and their demands for food increase, parents are forced to expand their foraging area 3-dimensionally: not only do they forage progressively farther away from the colony, but they also forage deeper (Ainley et al. 2004, Lescroël et al. 2010). When we tested whether prey selection in Adélie penguins differed between males and females, we found that males had significantly higher $\delta^{15}N$ values than females, which indicates that males consumed more fish than females. The diet of Adélie penguins nesting in colonies near Anvers Island west of the Antarctic Peninsula similarly varied between males and females, but only during 1 yr (in 2008) out of 3 yr of study (2007–2009; Gorman et al. 2014). Sexual segregation in diet and location appears to be more common in sexually dimorphic seabird species (Phillips et al. 2011), although a few monomorphic species also show dietary variation between sexes (e.g. common terns *Sterna hirundo* [Nisbet et al. 2002], northern gannets *Morus bassanus* [Lewis et al. 2002] and thin-billed prion *Pachyptila belcheri* [Quillfeldt et al. 2008]). But even small differences in body size between males and females in pursuit-diving seabirds have been found to influence their foraging behaviour and the prey they catch (Paredes et al. 2015). In Adélie penguins, males are larger than females (Ainley & Emison 1972, present study) and males often dive deeper than females (Lescroël et al. 2010). This would allow males to catch more silverfish *Pleuragramma antarctica* that tend to occur in deeper waters than crystal krill *Euphausia crystallorophias* in the southern Ross Sea, especially in late December

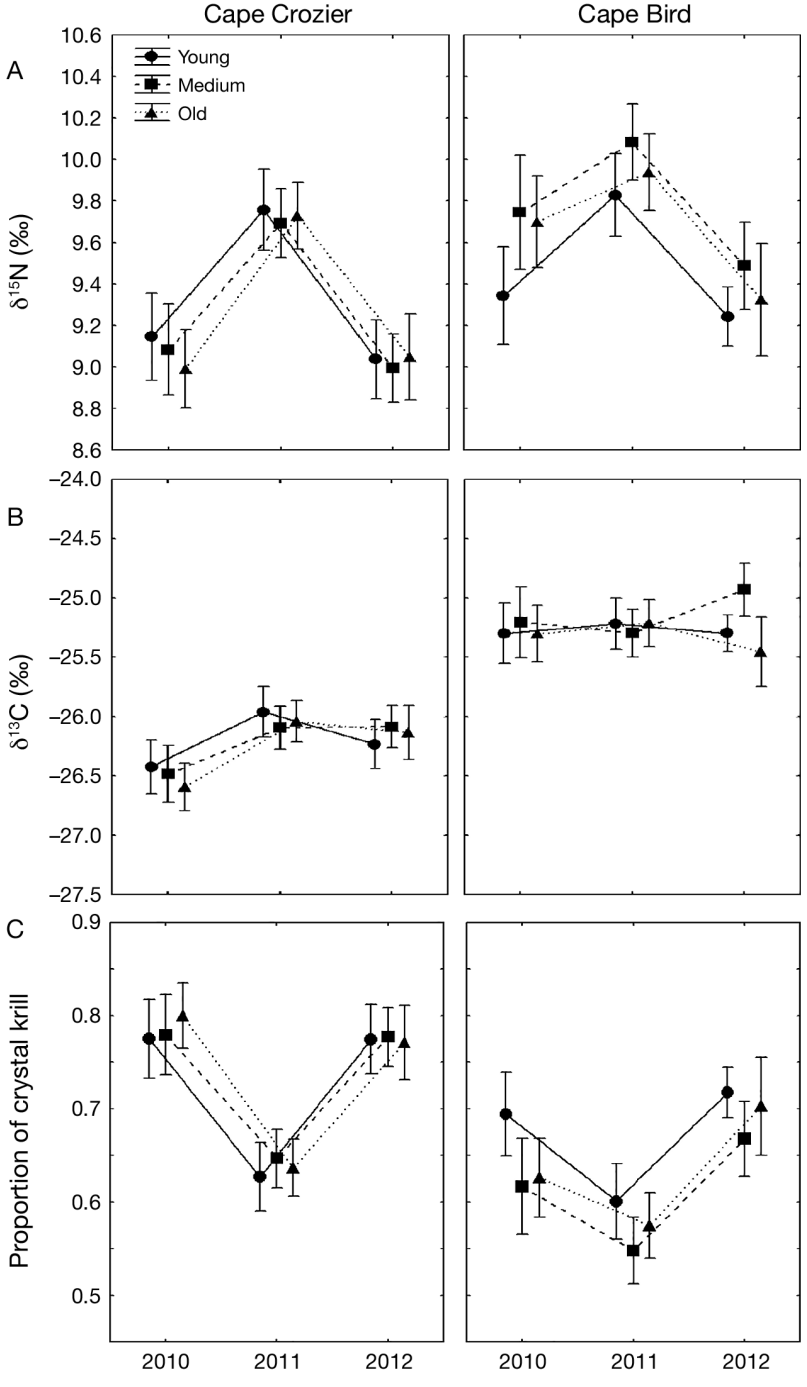

Fig. 5. Differences in (A) nitrogen isotope values ($\delta^{15}N$), (B) carbon isotope values ($\delta^{13}C$) and (C) proportions of crystal krill in the diet between young, middle-aged and old Adélie penguins. Means ± SD are shown

Table 3. Isotopic niche metrics of Adélie penguins from 2 colonies, calculated with the SIAR and SIBER packages

Symbol	Explanation	Bird	Crozier
N	Sample size	102	116
LOC	Location of centroid (mean $\delta^{13}C$, mean $\delta^{15}N$)	−25.2, 9.6	−26.2, 9.3
SEA	Area of the standard ellipse (isotope niche width)	0.69	0.39
SEAc	As above, corrected for sample size	0.69	0.39
SEAb	Bayesian standard ellipse area	0.68	0.38
NR	Trophic length (range in $\delta^{15}N$)	2.75	2.10
CR	Diversity of basal resources (range in $\delta^{13}C$)	2.40	1.63
CD	Niche width 2 (mean distance to centroid)	0.61	0.48
NND	Mean nearest neighbour distance	0.11	0.07

Table 4. Generalized linear models testing whether the diet, measured through $\delta^{15}N$, $\delta^{13}C$ and the proportion of crystal krill, differs between adult Adélie penguins of different age classes (young: 3–6 yr; middle-aged: 7–10 yr; old: 11–16 yr), with different breeding quality indices (BQIs; a continuous variable), from different colonies (Bird and Crozier), sampled in different years (2010, 2011, 2012); **bold values:** significant. SS: sum of squares; DF: degrees of freedom; MS: mean square

	SS	DF	MS	*F*	p (>*F*)
$\delta^{15}N$ (R^2 = 0.51)					
Intercept	16 289.95	1	16 289.95	144 604.2	<0.0001
BQI	0.001	1	0.00	0.0	0.91
Colony	6.04	1	6.04	53.7	**<0.0001**
Year	16.50	2	8.25	73.3	**<0.0001**
Age class	0.53	2	0.27	2.4	0.09
Colony × Year	0.76	2	0.38	3.4	**0.03**
Colony × Age class	0.99	2	0.50	4.4	**0.01**
Year × Age class	0.05	4	0.01	0.1	0.97
Colony × Year × Age class	0.23	4	0.06	0.5	0.72
Error	21.63	192	0.11		
$\delta^{13}C$ (R^2 = 0.65)					
Intercept	120 832.7	1	120 832.7	908 097.7	<0.0001
BQI	0.0001	1	0.0	0.0	0.98
Colony	46.2	1	46.2	347.1	**<0.0001**
Year	2.10	2	1.0	7.8	**<0.001**
Age class	0.40	2	0.20	1.5	0.23
Colony × Year	1.60	2	0.80	6.1	**0.002**
Colony × Age class	0.20	2	0.10	0.8	0.44
Year × Age class	1.20	4	0.30	2.3	0.06
Colony × Year × Age class	0.50	4	0.10	0.9	0.49
Error	25.50	192	0.10		
Crystal krill (R^2 = 0.58)					
Intercept	85.71	1	85.71	20 808.64	<0.0001
BQI	0.0005	1	0.00005	0.01	0.91
Colony	0.41	1	0.41	99.01	**<0.0001**
Year	0.69	2	0.34	83.71	**<0.0001**
Age class	0.02	2	0.009	2.39	0.09
Colony × Year	0.04	2	0.02	5.55	**0.004**
Colony × Age class	0.04	2	0.02	4.80	**0.009**
Year × Age class	0.002	4	0.0005	0.13	0.97
Colony × Year × Age class	0.009	4	0.002	0.58	0.67
Error	0.79	192	0.004		

and January (Ainley et al. 2015). The sexual segregation in diet was most evident at Cape Bird (Fig. 4A), where the overall niche was wider than at Cape Crozier (Fig. 3, Table 3). On the basis of this result, we suggest that the greater availability of multiple prey types at Cape Bird allowed penguins to broaden their diet. This was further supported by our findings that only at Cape Bird did diet vary between young, middle-aged and old birds, indicating that prey diversity in the Cape Crozier foraging area was limited in all 3 yr, and penguins at this colony had to compete for mostly one dominant food resource, crystal krill. In an earlier analysis of diet using stomach flushing, adult penguins at Cape Bird were found to have higher proportions of krill in their diet than those at Cape Crozier (Ainley et al. 2003). Stomach flushing provides a brief snapshot of the diet acquired during one foraging trip, while the stable isotope approach reflects assimilated prey over 3–4 wk (Barquete et al. 2013). Due to the different methodologies used, results from these 2 studies may not be comparable; nevertheless, the seeming reversal of diet between the earlier and the present study should be noted. In addition, the finding by Gorman et al. (2014) that Adélie penguin diet differed between males and females in one year, but not in 2 other years, and our results of sex- and age-related partitioning of diet in only 1 out of 2 colonies, suggest that diet segregation within a species is a plastic and adaptive response to competition for food resources, which in turn is dependent on the spatial and temporal availability of a variety of prey species.

To our knowledge, only 2 previous studies have investigated differences in diet among adults of varying ages (Forero et al. 2005, Pelletier et al. 2014). The diet of different-aged southern giant petrels *Macronectes giganteus* did not vary (Forero et al. 2005). Similarly, no differences in $\delta^{13}C$ and $\delta^{15}N$ values could be detected between middle-aged (5–11 yr) and old (>11 yr) male and female little penguins *Eudyptula minor*; however, middle-aged females had the largest isotopic niche (highest SEA_C) and middle-aged males the smallest, while old males and old females had intermediate niche sizes (Pelletier et al. 2014). At Cape Bird, middle-aged (age 7–10 yr) Adélie penguins consumed significantly more fish than old (11–16 yr) and young (3–6 yr) penguins. In this species, foraging proficiency increases with age and remains high even in older age (Lescroël et al. 2019). There is some evidence that foraging performance of older and more experienced birds explains an increased breeding performance with age in a number of long-lived species (e.g. Daunt et al. 2007, Limmer & Becker 2009). Experienced breeding pairs of European shags *Phalacrocorax aristolelis* were more proficient foragers and hence provisioned more food to offspring than first-time breeders (Daunt et al. 2007). In common terns *Sterna hirundo*, experienced parents were more successful in feeding their chicks, and while they provided the same prey to their offspring as did first-time breeders, experienced breeders delivered a higher proportion of energy-rich prey (Limmer & Becker 2009). In the southern Ross Sea, silverfish is energetically and nutritionally more rewarding prey for Adélie penguins than crystal krill (Hodum & Hobson 2000, Ainley et al. 2003, Lenky et al. 2012). There is also evidence that more fish in the diet of penguin offspring is beneficial to their growth and survival (Chapman et al. 2011, Whitehead et al. 2015, Jennings et al. 2016, Ainley et al. 2018). Hence, we expected that parents of high breeding quality would preferentially feed on fish to provision themselves and their growing offspring more appropriately. Although we found that old birds fed more on fish than young birds at Cape Bird, we did not find any evidence that better breeders (independent of age) consumed a more fish-rich diet than poorer breeders. As we only investigated the diet of parents (and not simultaneously the diet of their chicks), it is possible that adults of high breeding quality provision their chicks selectively with a high trophic level diet (i.e. with a higher proportion of fish), while their own diet remains similar to the diet of adults with a lower breeding quality. Adélie penguins from Adélie Land, Antarctica, fed their chicks on a higher trophic level diet than themselves ($\delta^{15}N$: 10.2 ± 0.8 versus 9.0 ± 0.2‰; Cherel 2008). This may also be the case in the Ross Sea region, whereby parents that are consistently better at raising offspring feed their chicks on a fish-rich diet. A study comparing diets between high- and low-BQI parents and their chicks is necessary to test this possibility.

4.2. Differences in diet between colonies and among years

As this study set out to test whether certain individuals can overcome colony-induced or annual foraging challenges, we included both intrinsic factors (sex, age, breeding quality) and extrinsic factors (colony, year) that may explain diet in Adélie penguins. Although the 2 colonies are only 75 km apart, the diet of penguins varied considerably between them: penguins at Cape Crozier, where sea ice cover was less than 20% during the study period in all 3 seasons, consumed consistently a lower proportion of fish (lower $\delta^{15}N$) than penguins at Cape Bird (Fig. 4A,C). Our nitrogen stable isotope values of 9.31 ± 0.45‰ for Adélie penguins at Cape Crozier and 9.60 ± 0.48‰ for penguins at Cape Bird are slightly higher than those reported for Adélie penguins breeding in Adélie Land (9.0 ± 0.2‰), which fed predominantly on crystal krill (Cherel 2008). Values in the present study were also higher than those of the 1996–1998 study, when Cape Bird penguins were feeding on more krill (Ainley et al. 2003). We also found significant differences in the $\delta^{13}C$ values between the colonies, whereby penguins at Cape Crozier had consistently lower values than those at Cape Bird (Fig. 4B). This suggests that penguins at these 2 colonies foraged in different habitats that possibly vary in their proximity to the most productive portion of the shifting marginal ice zone (MIZ; Smith & Nelson 1985), and which may have been responsible for the difference in prey species composition. While the foraging area of Cape Crozier was within the MIZ of the Ross Sea Polynya, where most sea ice had disappeared by the months of our study, the Cape Bird foraging area was within the MIZ of the McMurdo Sound Polynya and still had an active, productive ice edge. Our findings are consistent with those of Gorman (2015), who investigated the diet of Adélie penguin chicks at the crèche stage at 3 colonies (Anvers, Avian and Charcot Islands) within the western Antarctic Peninsula (WAP). Chicks on Anvers Island, the most northern island, where sea ice was the least prevalent, had lower $\delta^{13}C$ values than those in the more southerly

colonies (Avian and Charcot Islands) (Gorman 2015). Moreover, $\delta^{15}N$ values increased with latitude (from the most northern colony, on Anvers Island, to the most southern colony, on the Charcot Islands) and the penguin food web also became isotopically wider as sea ice coverage increased (Gorman 2015). The abundance of silverfish increases with latitude and the prevalence of sea ice along the WAP (La Mesa et al. 2015), consistent with the stable isotope pattern in the diet of penguins. Although Cape Crozier and Cape Bird are less distant from each other than Anvers Island and the Charcot Islands (~700 km), we found a similar trend of increasing stable isotope values in relation to sea ice.

Besides differences in diet between the colonies, we also found high inter-annual variation in diet. In 2011, penguins at both colonies foraged on a lower proportion of crystal krill than in 2010 and 2012, although this inter-annual variation in diet was more pronounced at Cape Crozier than at Cape Bird (Fig. 4). Unfortunately, there is almost no information on inter-annual variation in the abundance, spatial availability or age structure of either crystal krill or silverfish in the Ross Sea, except for some information about where larval silverfish are most abundant (La Mesa et al. 2010). As silverfish is an ice-obligate species (La Mesa & Eastman 2012), their spatial and temporal abundances are likely linked to sea ice cover (La Mesa et al. 2015), which can vary significantly between years in the Ross Sea (Arrigo & van Dijken 2004). In addition, foraging whales and penguins decrease local abundances of crystal krill and silverfish (Ainley et al. 2006, 2015), and this within-season depletion of prey is considerably more pronounced in the proximity of large penguin colonies, such as Cape Crozier (Ainley et al. 2004). Overall, we show that the diet of Adélie penguins varied significantly between locations and years, providing an ideal scenario for testing whether certain individuals can overcome spatial and temporal resource constraints. Given the observed effects on diet, the present study clarifies that Adélie penguins are largely at the mercy of annual, seasonal and local abundances of prey, with only some individuals able to selectively forage for certain, more nutritional prey if a variety of prey is available in the proximity of colonies.

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